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THE BEHAVIOR OF LIMPETS WITH PARTICULAR REFERENCE TO THE HOMING INSTINCT

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INTRODUCTION

More than casual interest attaches to the behavior of animals that possess marked homing ability and it is of importance that the detailed behavior of such forms be recorded. Certain investigators have maintained that homing is a type of behavior set apart from the ordinary reactions of animals and in an attempt to explain the homing ability have hypothecated a sixth sense or some even less demonstrable factor. No morphological foundation for such hypotheses seems discoverable and we must, therefore, look to a detailed examination into the behavior of homing animals for an explanation of the homing instinct. We need not, I believe, look for this explanation to result from some startling discovery, but rather, expect it to emerge from an apparent hodge-podge of miscellaneous facts relating to animal behavior. It is not likely that the homing instinct is peculiar to any particular type of organism but it is rather inherent in all protoplasm. In the process of evolution certain groups of animals seem to have developed the homing ability to a higher degree than have other groups, but this is true for all other types of animal behavior. In the so-called homing species, the variations in the ability of the individuals to home are so marked and the instances of homing behavior in so-called non-homing species are so numerous, that one cannot but believe that animals differ quantitatively rather than qualitatively in the possession of this instinct.

Among the invertebrate forms, the limpets are particularly interesting in connection with investigations of the homing instinct. These animals possess none but the simpler types of sense organs yet show marked ability in finding their way back, at regular intervals, to a given resting place or "home." The observations herein recorded possess only passing biological interest when taken singly but it is felt that as a whole they may be of some assistance to other observers who are interested in limpets and their homing behavior. They were made, during the winter of 1915, at which time the author was staying at the Scripps Institution for Biological Research, which institution is located at LaJolla, California.

PRESENTATION OF DATA

The rocks, on the beach to the north of the Scripps laboratory, are thickly populated with limpets belonging to three genera and to at least six species. The genus Acmea is represented by the species *patina*, *persona*, *scabra*, and *spectrum*. The two other genera are Lottia and Fisurella; of these genera one species each is common, namely, *L. gigantea* and *F. volcano*.

1. *Distribution of the limpets.*—The limpets show marked generic and specific differences in their distribution on the beach. The most common species is *Acmea scabra*, which occurs in great numbers on all the rocks of the high and middle beach. The other species of Acmea are not so numerous nor so widely distributed as *scabra*. *A. patina* and *A. persona* are found with scabra on the middle beach while *A. spectrum* is usually more abundant on the lower beach. Lottia *gigantea* occurs only in situations exposed to the main force of the waves. Specimens of *Fisurella volcano* were frequently collected from the kelp-covered rocks that are barely exposed at low tide. A large per cent of such specimens were living in the hollow halves of the deserted bivalve shells that are firmly cemented to these rocks.

2. *General behavior of the limpets.*—The movements of the limpets are largely controlled by the tides. When the tide is out, they remain practically motionless on the rocks and present no visible sign of life. With the first dash of spray from the incoming tide they begin to move and are apparently active until the water recedes once more.

3. *The clinging of the limpets.*—Limpets are completely helpless when removed from the rocks. If dropped into still water, they invariably fall with the shell side down and unless righted by some external force will remain in this position, perfectly helpless, until dead. Individuals dropped into an aquarium at first made attempts to right themselves by stretching the foot up out of the shell. They were unable to turn over, however, and after 48 hours, all were dead.

This helplessness when detached, suggests that the marked ability to survive and multiply, which limpets possess, must be accompanied by an ability to prevent themselves ever being detached. To ascertain with what force they cling to the rocks, a pair of miniature, three-clawed tongs was made from large fish hooks, and employed in pulling the animals from their attachments. The sharpened points of the claws of the tongs were hammered into knife edges so that they could be easily inserted under the edges of the limpets' shells. With the limpet attached to the rock the tongs were adjusted in such a manner, that the animal could be lifted directly from its resting place by a pull, perpendicular to the rock's surface. A spring balance, that had previously been calibrated, was hooked into the eye ends of the tongs and a steady pull detached the limpet from the rock. By noting the figure reached by the indicator of the scale just as the limpet left the rock, the pull necessary to overcome the attachment of the limpet's foot was determined.

Limpets of various sizes and species were tested with the following results. No marked specific differences in clinging power were observed, the recorded differences being directly correlated with the area of the foot of the individual.

The figures show a variation from 5 lbs., the force required to detach the smallest limpet tested, to 48 lbs. for the largest. The foot of the smallest animal was 2.2 cm. long and 1.8 cm. wide, while that of the largest was 4.3 cm. by 3.2 cm.

It was noted that the limpets need not be attached to a smooth surface, but rather the contrary, if they are to display their best clinging ability. Limpets that were attached to barnacle covered rocks seemed to cling with fully as much force as those attached to the fairly smooth, but wave eroded, rock surface. When limpets were pulled from barnacle encrusted rocks, the barnacles with which the foot of the animal was

in contact were frequently detached with the limpet and remained attached to its foot. In many instances, the limpets were attached to the barnacle covered rocks in such a way that one could actually see daylight between the rather loosely set barnacle shells under the animal's foot. Even in these cases, the pull required to detach the limpet was very little if any less, than that required for the other situations and usually the limpet did not leave the rock, without bringing the barnacle cases with it. On the other hand, limpets pulled from glass plates came off with the application of about one-half the force necessary to detach them from the rocks. Calculations, based upon the clinging power of the limpets, indicate that the large Abalones (another gastropod mollusc much larger than the limpets) that are numerous along the coast of southern California can cling with a power equal to 1100 pounds weight. One who has attempted to pull them from the rocks may well credit them with this great adhesive power.

4. *Reaction of limpets to environmental factors.*—A large number of readings was taken as to the position which the limpets assume on the rocks, in relation to the current made by the waves, to the pull of gravity, and to the direction of the sun's rays. The readings were taken daily for three weeks. The following table summarizes the results.

Reaction to—	Positive	Negative	Indifferent
Current	450–51%	321–36%	117–13%
Gravity	334–54%	203–33%	73–13%
Light	285–37%	266–36%	199–27%

The figures indicate a strong positive reaction to current and gravity but none to the light. It is readily noted that limpets do not occupy the sunny sides of rocks but this is probably a negative reaction to temperature rather than to light. Experiments with light gradients will probably indicate a selection of a medium light upon the part of these limpets. In the above experiments the reaction was to direction of rays rather than to intensity since the orientation of the animals, i.e., whether facing toward or away from the sun, were the only data recorded.

5. *The homing instinct.*—Observations, continuing in some cases for a little over a month, were carried on, to determine the daily relation of the different species of limpets to a given resting place on the rocks. The idea was, first, to determine whether or not any or all of the species possessed a definite

homing ability, and second, to ascertain something as to the nature of such ability should it be present.

All of the limpets under observation were found to move about, at periods of high tide only. The movement began with the first wetting from the incoming tide, and proceeded more or less continuously, till the retreating water left the animals high and dry once more.

About 30 limpets, representing four species of Acmea and the one species of Lottia, were marked by filing Roman numerals into their shells. This method made it necessary to mark the animals but once, for the grooves could be filed quite deep into the shells without injuring the animals in the least.

The limpets were chosen, so that all the possible situations were represented. Some were on horizontal rocks, some on vertical ledges; some were exposed, some were not, etc. The spot on which the limpet was resting, on the first day of observation, was enclosed in a small rectangle scratched into the rock and alongside this rectangle the roman number which the limpet carried was also filed into the rock. From day to day the location of each limpet was determined by referring it back to this numbered rectangle. The daily positions were plotted on squared paper and the resulting graph, together with the field notes, constitutes the permanent record of the limpet's activities. The graphs that follow will furnish an idea of the behavior of the different species of Acmea, during the period of observation.

Figure 1 indicates the wanderings of an individual of the species *Acmea spectrum*, during a period of 27 days. It is at once evident that this animal did not habitually return to any given spot on the rock, when the tide retreated. It will be noted further that there was even a tendency to change localities. This individual was situated on a flat rock, where the waves washed it much of the time.

The readings represented in Figure 1 were taken but once a day and it soon became obvious that there was considerable to be learned by observations made at more frequent intervals. To check up this point a number of days was spent taking hourly observations upon individual limpets. Figure 1A shows the result of hourly readings upon the individual referred to in Figure 1. Figure 1A, from its appearance, might represent a series of 5 consecutive readings taken from some part of Fig. 1,

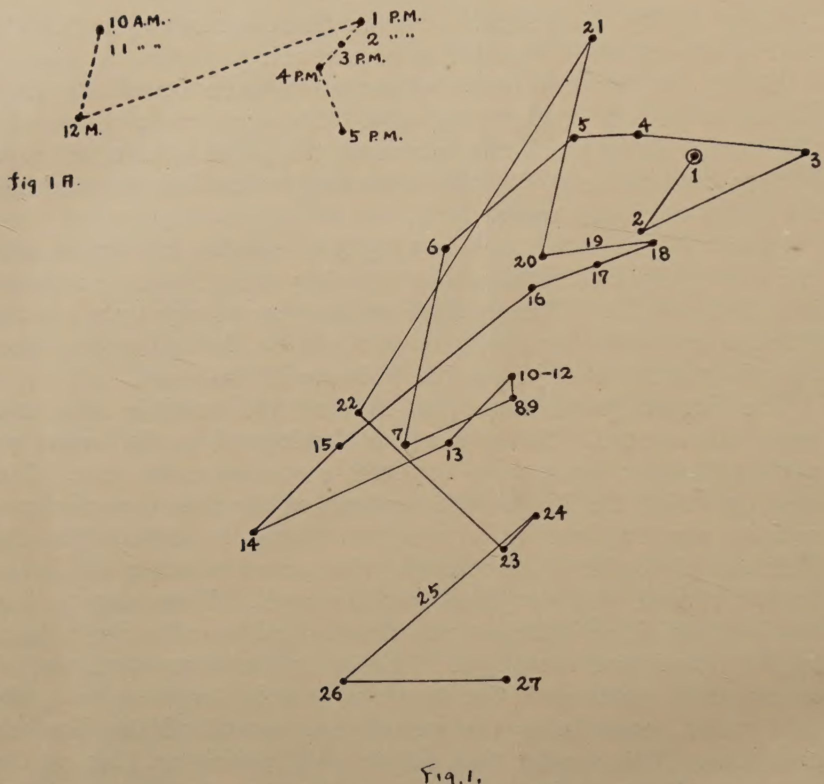

FIG. 1.—Graph of the movements of a non-homing individual of *Acmea spectrum*. Observations made once a day for 27 days.

FIG. 1A.-Graph of the movements of the limpet whose path is shown in Fig. 1. The movements shown in Fig. 1A took place on the 15th day. Readings hourly.

yet it is actually part of the path travelled between the 15th and 16th readings. It is evident that the limpets move about a great deal more than the graph (Fig. 1) would lead us to believe. However, the fact remains that this particular limpet showed no signs of homing, during the period of observation.

Figure 2 indicates the behavior of another individual of *Acmea spectrum*; this individual was situated upon the same flat rock with the individual discussed above and several times the two animals were but a few inches apart. Figure 2, however, shows a very different type of behavior from that indicated in Fig. 1.

The limpet, whose path is traced in Fig. 2, shows a marked tendency to return to some particular spot, after its daily wan-

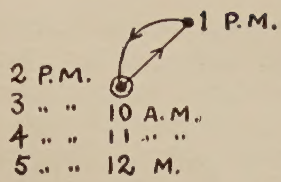

fig. 2A.

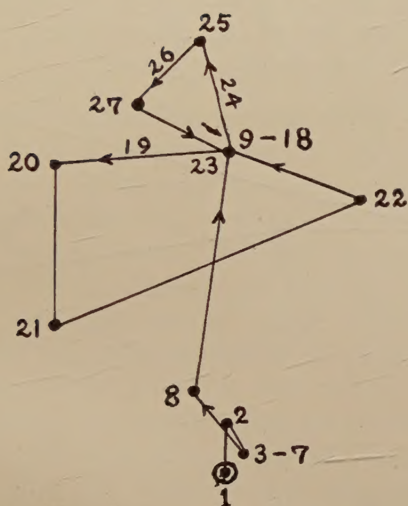

fig 2

FIG. 2.—Graph of the path followed by an individual of *Acmea spectrum* during a period of 28 days. Readings once a day.
FIG. 2A.–Shows the extent to which the same limpet moved during a seven hour period on the 14th day.

derings. During the 28 days over which the observations extended, two principal spots were occupied. Both were small depressions in the rock surface, into which the shell of the limpet fitted rather snugly. Figure 2A indicates the extent of this animal's movements during a seven-hour period of observation on March 9, which was the 14th day shown in Figure 1. Note that the limpet left the depression for only one hour and that during this time it moved out and back, along a path which represents an egg-shaped oval.

The other species of Acmea showed the same type of behavior as that indicated for *spectrum*; they showed also, the same wide variation in the behavior of different individuals. Figure 3 is a graph plotted from the data furnished by an individual of *Acmea scabra*. This individual was located on a vertical face of rock and was subjected to the direct dash of the waves.

It will be noted that the animal whose behavior is indicated in Fig. 3 was found in the same spot from the 5th to the 12th day and then, after moving about for four days, settled down again and on the 30th and last day of the observational period was still to be found in this second resting place.

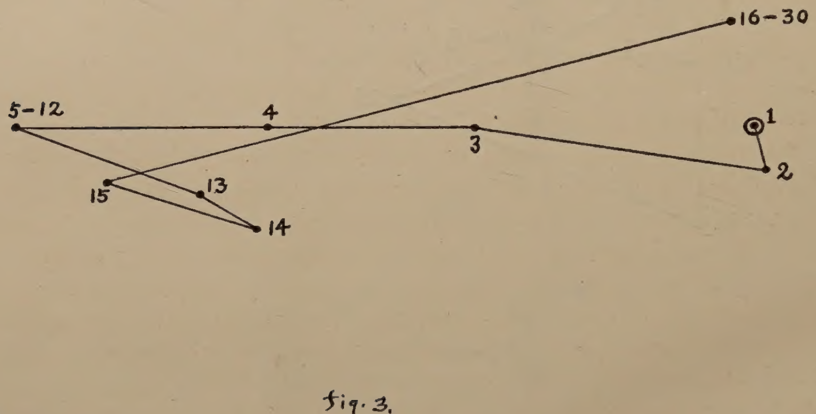

Fig. 3.—Graph of the movements of an individual of *Acmea scabra*. Readings once a day.

The foregoing experiments indicate that the limpets of the genus Acmea possess a rather definite homing instinct which is displayed by certain individuals more than by others; the other data serve to confirm this view.

The species *Lottia gigantea* was found to be a very consistent homer with the individual variation reduced to a minimum. Seven individuals of this large species were marked and observed daily for 25 days. These animals were located on the exposed side of an immense boulder, and were subjected to the direct influence of the incoming waves very soon after the turning of the tide. The exposed position made observation of actual movements rather difficult, for like the other species, *Lottia gigantea* moves only when moistened by the waves.

The low-tide observations upon the seven individuals of

Lottia gigantea showed that without exception, these limpets returned daily, each to a given depression or other recognizable spot on the rock's surface. The observations on the limpets while they were moving, i.e., while the tide was coming in, showed that they left their resting places very soon after the first dash of spray had thoroughly wet them, and that they crawled about continuously as long as the observations were continued. A given individual usually left its resting place in the direction in which it was headed. It would now crawl across the surface of the rock, which was usually thickly covered with barnacles. The path taken was not straight away from the homing point but curved either to the right or to the left. After going a certain distance, usually but 5-6 inches at first, the limpet would turn almost around and after completing the other side of an oval, such as is shown in Fig. 2A, would be back at its resting place. Instead of settling down, however, the animal usually started out immediately upon another journey, which was likely to be longer than the first. From all that could be seen this procedure was kept up; each successive journey was longer than the last and on each subsequent trip the path became more and more irregular until the animal appeared to be merely wandering about in the vicinity of its resting place.

The greatest distance that any animal of this species was found from its home, was 16 inches. This individual was still 12 inches away, when observations had to be discontinued, but it was found at home as usual the next day.

No experiments were performed to determine the ability of these limpets to return to their resting place when transferred bodily to a distance, though there can be little doubt but that they would be able to do this to a limited extent, just as has been shown by Morgan for certain species which he has unfortunately failed to name.

In general, the writer was impressed with the fact that the limpet offers a much easier subject for the investigation of the homing instinct than is presented by the highly motile forms, such as the insects and birds, and at the same time it seems possible that in the investigation of the instinct which guides the limpet over its few square inches we may find a clue which will help us to explain the ability that enables birds to orient themselves over hundreds of miles.

LITERATURE FOR 1916 ON THE BEHAVIOR OF THE LOWER INVERTEBRATES

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In studying the effect of different electrolytes and cane sugar on rheotaxis in Asellus, Allee (1, 2) finds that in many respects the substances used affect the positiveness of the rheotactic reaction in the same way that they affect many other physiological processes. The antagonism between KCl and $CaCl_2$ is particularly well marked. The former increases and the latter decreases the percentage of positive reactions and shows a wholly similar effect on the rate of metabolism as measured by resistance to the cyanides and production of CO_2. The conclusions are based on experiments on over a thousand individuals.

Allen (3) gives some notes on the migrations, etc., of the spiny lobster, *Panulirus interruptus*.

In a study of the action of Schumann rays on living organisms, Bovie (4) gives an account of the response of certain amoebae and infusoria to this region of the spectrum.

The Journal of Animal Behavior (5) publishes a translation of Buddenbrock's "Die Tropismentheorie von Jacques Loeb" (*Biol. Cent.*, **35,** 481-506). The original article was noted in this review for last year.

Attention is called to Cary's (6) study of the influence of the marginal sense organs on the rate of regeneration in *Cassiopea xamachana*. A preliminary summary of this work was given in this review for last year.

Crozier (7) is of the opinion that the behavior of *Holothuria captiva* when illuminated on two sides is such as to show "that photic stimulation in this animal depends upon the amount of light falling upon the sensitive surface, and is independent of the angle of incidence." In working on *Stichopus moebii* he (8) finds that the mechanism for the pulsation of the cloacal chamber is locally contained, i.e., within the cloaca. He then takes up a study of the relation of certain chemicals, temperature,

etc., to this rhythmic pulsation. The same author (9) gives a note on the behavior of the barnacle *Conchodermata virgatum* and another (10) on the immunity coloration in the nudibranch, *Chromodoris zebra*.

In studying the feeding habits of certain pelagic copepods, Esterly (11) finds that the head and appendages of *Calanus finmarchicus* produce water currents which carry floating particles toward the mouth. These currents are directed chiefly by a trough-like arrangement of the bristles of the anterior maxilliped. The particles are formed into a pellet which is held behind the mouth and from where it is passed into the oesophagus. The author then takes up a study of the various food forms found in the digestive tracts of various copepods.

Grave (12) takes exception to Kellogg (*Jour. of Morph.*, **26**, 625-701), who is working on the feeding of Lamellibranchs comes to the conclusions that " Volume alone determines whether the collected foreign matter that reaches the palps shall proceed to the mouth or shall be sent from the body on outgoing tracts." Also, as corollaries to this conclusion, that a Lamellibranch can feed only in comparatively clear water, can make no separation or selection of food particles, and has no mechanism for the reversal of the effective beat of the cilia. Grave gives some experiments on Ostrea which tend to show that they can feed in water which contains a large quantity of sediment, etc. He then collects certain evidence on other animals which shows that they can make a selection of food by a control of the beat of the cilia and suggests that the same may hold in the case of Ostrea. Kellogg (16) answers this criticism in a polemic entitled " Opinions on Some Ciliary Activities."

Jordan (13), in a study of the irritability of the muscles and the influence of the nervous system on the musculature of certain holothurians, gives a description of certain reactions of these animals.

Kanda (14) finds that the marine snail *Littorina littorea* is negative in its reaction to gravity, but that this reaction is influenced by the fact that the animal is also negative to light. The author finds that in sea water the angle of inclination (to the horizontal) of the surface on which the snails move, has a marked influence on the percentage of positive and negative animals,—the larger the angle, the larger the number of nega-

tively geotropic animals. The presence of air or sea water, the presence of direct sunlight, and the character of the surface on which the snails move, all have some effect on the reactions to gravity. "From the experimental results which the writer has obtained, he concludes that neither the mechanical theory, nor the pressure theory, nor the resistance theory is adequate to explain the phenomenon of the negative geotropism of *Littorina littorea* but a physiological one, that is, the statocyst or statolith theory. This theory is the more likely since these snails have statoliths. The writer, however, has no direct evidence, at present, in favor of the statolith theory." A similar conclusion (15) concerning the statolith theory is reached after a study of the reactions to gravity of certain freshwater snails.

Lankester (17) gives certain arguments against the conclusion, set forth by Carpenter (1874) and Heron-Allen (1915), to the effect that the behavior of the Foraminifera is evidence of intelligence in these organisms.

In continuing their work on the relative efficiency of various parts of the spectrum for the photic reactions of plants and animals, Loeb and Wasteneys (18) give the following regions of the spectrum as being the most efficient for the following organisms: *Eudendrium ramosum*, 460-480$\mu\mu$; *Euglena viridis*, 460-490$\mu\mu$; *Arenicola larvae*, about 495$\mu\mu$; *Chlamydomonas pisiformis*, about 535$\mu\mu$; *Balanus eburneus larvae*, 560-578$\mu\mu$. These results were obtained by subjecting the organisms simultaneously to two beams of monochromatic light from different directions and then comparing their distribution in the two beams.

Löhner (19) has made some feeding experiments on leeches by letting them attach themselves to a piece of fresh animal hide which has been fastened to the end of a tube containing blood. After the animals have thus attached themselves, in a normal manner, the blood in the tube is removed and various solutions substituted. In experimenting with the so-called four types of gustatory solutions (salty, sweet, sour, and bitter) the author finds that the animals show a "detaching" or "repulsion" reaction at the following percentage solutions: Sodium chloride 7%; Cane sugar 5%; Quinine sulphate 0.08 to 0.1%; Hydrochloric acid 0.09 to 0.1%; and Potash 0.08 to 0.9%. No such reaction follows from pure water.

Following a description of the eye-spot of *Gonium pectorale*, Mast (20) gives an account of the process of orientation to light in this organism. Orientation is direct (the colonies never turning in the wrong direction) and in positive colonies it is brought about by an increase in the activity of the flagella of the zooids on the side away from the light. This is held to be dependent upon the time-rate of change of illumination on the tissue which is sensitive to light.

Mast and Lashley (21) find that there is no continuous production of a feeding-cone in free-swimming Paramoecia, Stentor or Spirostomum. The water sucked toward them is through so short a distance (probably not over twice the length of the cilia) as to make such currents of no appreciable value in testing unfavorable environment ahead of the specimen. The feeding-cone is produced only under special conditions.

Mast and Root (22, 23) find that the pseudopods of *Amoeba proteus* in forming a food vacuole about a Paramoecium sometimes come together before they are fully extended, thus cutting the latter in two. The authors estimate that if this process is due solely to a change in the surface tension on the surface of the Amoeba it would have to be higher than 383 dynes per cm.^{2} at the very least and that it probably would have to exceed 1,118 dynes per cm.^{2} As the surface tension of protoplasm is only about 50 dynes per cm.^{2}, they conclude that if surface tension plays a part in the division of Paramoecium it is a very insignificant rôle.

Maupas and Seurat (24) give a note on the copulation of certain nematodes.

As a result of a study of certain reactions of *Cassiopea xanachana*, Mayer (25, 26, 27) gives some interesting suggestions as to the nature of nerve conduction in this organism.

Mendelssohn (28) finds that a leucocyte, in response to the stimulation of an electrical current, so changes its form as to produce one large pseudopodium which is always directed towards the cathode.

Metalnikov (29, 30) finds that the length of time that a given food vacuole will circulate in the body of Paramoecium is very variable. According to him this variability depends upon three factors: (1) The character of the specific stimulating substance,

i.e., the character of the food substance; (2) variations in the external medium; (3) the internal state of the organism.

Moore (31) maintains that Mast, in his work on *Gonium pectorale* (reviewed above) in which he holds that orientation to light is brought about by the increased activity of the flagella of the zooids furthest from the stimulated side, does not take into account the possibility that orientation may be brought about by the unequal activity of the two flagella of each single cell. The author's criticism is based on Moore and Goodspeed's study of the orientation of Gonium under the influence of a galvanic current.

In a study of the reaction of *Lumbricus* under the influence of a galvanic current, Moore and Kellogg (32) find that this animal at first directs both the anterior and posterior ends toward the cathode, thus assuming a horse-shoe shape. Owing to the fact that the anterior end is more active than the posterior, the worm ultimately succeeds in reaching the cathode. The author is of the opinion that these reactions are in accord with Loeb's theory of galvanotropism.

Parker (33, 34, 35, 36, 37, 38) and Parker and Titus (39) have done some very interesting work on the reactions and structure of certain sea-anemones. This work constitutes a valuable contribution to the neuromuscular physiology of this group. It is, however, too extensive to more than mention in this review.

Rabaud (40) gives an account of the occurrence of the death-feigning reflex in a number of insects and myriapods. He (41) also gives a note on the nature of this reflex.

In a study of the relation of the body temperature of certain cold-blooded animals to that of their environment, Rogers and Lewis (42) find that the earthworm quickly adjusts itself to the temperature of a rapidly circulating environment while the clam does so less rapidly. After these animals have so adjusted their body temperature, it shows a very close agreement to the temperature of the given environment.

Schaeffer (43), in studying the food reactions of two species of Amoeba finds that, "A hungry amoeba will eat the same carmine grain several times in succession, but with each eating the grain becomes less attractive, until it is refused." This refusal, he holds, is very likely due to some change in the grain of carmine as a new grain is generally eaten if presented to the

animal. The animal usually rids itself of the carmine very quickly, by a more or less complete reversal of the direction of its movement. Grains of carmine are sensed by the Amoeba at a distance of at least 100 microns. The animals have a similar power of sensing egg white, uric acid and India ink at a distance. Daylight, acting continuously, has no effect on the food reactions. There is no way of predicting the size and shape of the food cup from the stimulating object alone. The author is of the opinion that the ectoplasm and endoplasm (of the granular species studied) react to such things as carmine in an opposite manner, the former being positive and the latter negative. In another paper the author (44) gives an account of the behavior of Amoeba to glass, carbon, tyrosine, egg albumen, peptone, etc.

Torrey (45) gives an essay on the physiological analysis of behavior.

Walton (46) finds that in *Paramoecium caudatum* there is an increase in the rate of locomotion in response to an increase in illumination. In animals from non-conjugating lines, 85% gave this response, whereas only 55% of those from conjugating lines showed it. This response to increased light intensity is only gradually effected. The response of a given specimen is the same to a given illumination irrespective of the light intensity to which the animal has been previously exposed, provided the specimen is given time to adjust itself to the new intensity. As has been the case with previous investigators, no evidence was found of a directive or orienting effect produced by the light.

According to Wenrich (47) *Anodonta fluviatilis* is sensitive to very slight decreases but not to increases in illumination. Such stimulation generally results in the closing of one or both siphons (seldom in closing the valves); the exhalant siphon being more sensitive than the inhalant. In continuing his work on some 18 marine species of bivalve mollusks, the author finds three classes: "(a) Those sensitive to both increase and decrease in light intensity (e.g., Mya); and (b) those sensitive to decrease only (e.g., Pecten); and (c) those sensitive neither to decrease nor to increase (e.g., Cumingia)." There is a perfect correlation in these species between sensitivity to light and the presence of pigment in the epithelium of the sensitive area. *Pecten gibbus* shows a vigorous reaction by closing the valves in response to an upward moving white card over a black background. As the

upward movement of the card in this case involves an increase in light intensity and as Pecten shows typical reactions only to decreases in intensity, the author is of the opinion that these experiments show that the eye of Pecten may form an image.

Willis (48) finds that fragments of *Amoeba proteus* which contain a nucleus exhibit essentially the same type of locomotion and orientation to light as do normal specimens. In enucleated fragments, however, locomotion is very imperfect and there is no evidence of orientation to a horizontal beam of light. The author is of the opinion that this regulatory influence of the nucleus is "brought about by some sort of an influence upon the attachment of the organism to the substratum."

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LITERATURE FOR 1916 ON THE BEHAVIOR OF SPIDERS AND INSECTS OTHER THAN ANTS

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TROPISMS AND RELATED PHENOMENA

Winn (119) thinks that certain butterflies exhibit phototropisms.

A trap net, with a bright lantern as a lure, was hauled across a field on a slowly moving wagon. A much larger variety of insects was captured than were enticed into stationary lure nets. Hence Holloway (48) concludes that a moving light has a greater attraction for insects than one that is fixed.

Runner (90) describes experiments upon the effects of roentgen rays on the cigarette beetle.

Richardson (86) finds that the house-fly is attracted by both ammonium hydrate and ammonium carbonate. He also notes (85) that the odor of ammonia attracts a varied dipterous aggregation; and that all of the species thus responding are known to spend at least part of their lives in some animal excrement. Since practically all animal excrement gives off ammonia, he concludes that it is probably the ammonia gas which attracts flies to manure.

In the behavior literature of today, the tropism hypothesis holds a prominent place. There have been protests against its universal application; but, so widespread is the impression that the complex acts of insects can be resolved into tropisms that these protests are popularly considered the anthropomorphic effusions of non-critical minds. Each year the number of students who are unwilling to subscribe unreservedly to the tropism hypothesis increases. This year Pictet (79), after a critical analysis of numerous experiments, concludes that the locomotions of insects are not phototropisms. According to him: "The tropism theory does not harmonize with the variety of ways an organism responds to a given stimulus. . . . It has not been demonstrated that the ascending and descending

flights of insects are determined by the direction of the rays of light; on the contrary, their movements appear to be regulated by voluntary acts, which are induced by physiological needs, fright, interest, habit, search for the female, etc. . . . Insects do not orient themselves towards either natural or artificial light in response to a physico-chemical force exerted by the rays of light, but by voluntary and conscious acts aroused by various conditions in the environment. . . . Responses to heat and cold are not tropisms, but reactions to sensations."

FEEDING AND HUNTING BEHAVIOR

Baker and Turner (6) describe the feeding habits of the green apple aphis; Barbey (8), of the larva of the long-horned beetle *Cerambyx heros*; Brittain and Godderham (12), of *Depressaria heraclina*; Clausen (14), of some Californian Coccinellidae; Cory (17), of the Columbine leaf miner; Cushman (22), of the apple red-bugs; Hayes (41), of the maize bill-bug; Herrick (43), of the cherry-leaf beetle; Hungerford (49), of Sciara maggots; Osborn (70), of several Maine leaf hoppers; Schoene (92, 93), of the seed-corn maggot and of the turnip maggot; Warren (113), of the Hawaiian dragon flies; and Whitmarsh (117), of *Apateticus maculiventris*.

Sanders and Fracker (91) find that the May beetles of Wisconsin feed upon the roots of plants and the fragments of the same; but that they will not eat moist bran nor flour paste. They feed only during the heat of the day; but there is no daily migration such as cut worms have.

Watson tells us (114) that the noctuid moth, *Anticarsia gemmatilis*, which feeds on the kudxy vine and velvet beans, forages continuously both day and night, stopping only to moult.

Essig (28) mentions a moth which feeds upon coccids.

According to McGregor (63), the privet mite feeds upon privet, Boston ivy, golden rod, palm, orange, lemon, etc.

Davis and Satterwait's investigations (23) show that the true army-worm feeds at first on its egg shells; later upon the parenchyma of the corn leaf and finally upon all the tissues of the leaf.

Paddock (72) informs us that the turnip louse feeds upon turnips, radishes, mustard, rape, collards, rutabagas, cabbages, kale, kohl-rabi, beans and lettuce.

Tower's experiments (105) demonstrate that the parasitized caterpillar of *Cirphis unipuncta* eats half as much as the normal larva.

Felt (30) finds that the feeding habits of the codling moth vary with the season. The early brood bores deep; the later keeps near the surface of the fruit.

Sell (94) has experimentally demonstrated that the 12-spotted cucumber beetle can change from an exclusive diet of one kind to a different menu, without being injured.

In 1843 Hutton[1] described the feeding habits of a large false-spider which he claimed was carnivorous. The blood-sucking habit is so universal among the Arachnida that J. H. Comstock doubted the correctness of Hutton's statements. He writes:[2] "Captain Hutton states distinctly that the *Galeodes* observed by him consumed an entire lizard except the jaws and parts of the skin. Other instances in which solpugids are supposed to have eaten their prey are given by Rev. J. J. Wood, in his 'Natural History Illustrated,' and quoted by Murray. Still, it is believed that solpugids take only liquid food, which they suck from the bodies of their victims." Turner (110) has demonstrated that the solpugids are carnivorous. Our American form, aided by the scissors-saw-like movements of its powerful jaws, pulpifies and devours all parts of captured insects except the chitin. Normally our form feeds only on live prey; but it may be caused to eat dead insects, by artificially inducing such insects to move.

MATING BEHAVIOR

Rohwer (89) discusses the mating of saw-flies; Somes (100), of the clear-winged moths *Seisia rileyana* Dry. and *Cassida solani* Boh., and Watson (114), of the noctuid moth *Anticarsia gemmatilis*.

Baker (6) states that the green apple-tree aphis mates within two days after reaching maturity and remains in coitu twenty-five minutes.

Hutchison's experiments (50) show that the house-fly mates as early as the first day after emergence and as late as the forty-seventh.

[1] Hutton, G. T. Observations on the Habits of a Large Species of *Galeodes*. *The Ann. and Mag. of Natural Hist.*, vol. XII, pp. 81-85.

[2] Comstock, J. H. The Spider Book, 1911, pp. 32-39.

Although the organization of termite society resembles in many respects that of the ants and bees, yet their mating behavior is quite different. According to Snyder (99) the sexual relations of termites is continuous. Copulation is repeated at regular intervals for several years.

The advent of the tropism hypothesis induced students of behavior to look upon the hovering of insects as a tropism, usually an anaemotropism. In 1908[3] it was demonstrated that the hovering of one species of mining bees is a mating device. In 1911 Perez[4] reported observations which induced him to conclude that the hoverings of several species of flies are preliminary to mating. Records of the field work of Turner (110A) on the ant *Lasius niger* and of Rau (82) on the solitary bee *Colletes compactus* show that the mating of both of these forms is preceded by a riotous sun-dance of the males. Occasionally females appear in the midst of the dancers. Then certain males drop out and mate. Apparently, in many cases, we must look upon the hoverings of insects, not as tropisms, but as prenuptial dances of the males.

According to C. L. Turner (111): "1. Movements preliminary to copulation are fairly constant in each group of Orthoptera and vary from simple (Mantidae, Phasmidae and Acrididae) to complex (Blatidae, Gryllidae, and Locustidae). 2. There is sex discrimination in the males of all forms. The female plays an aggressive part and displays discrimination of sex in some groups while in others she is absolutely passive. 3. There is a typical mode of copulation for each family of the Orthoptera. In the Mantidae, the Phasmidae and the Acrididae there is a superposition of the body of the male. In the Blatidae and Gryllidae there is a superposition of the body of the female. In the Locustidae there is an end to end copulation. 4. Families represented by the least number of sub-families are highly specialized; while those represented by the largest number of subfamilies have a generalized type of reproductive behavior. 5. A comparison between a classification based upon the reproductive behavior and one based upon paleontological evidence shows a striking agreement and suggests that the different types

[3] Turner, C. H. The Sun-Dance of Mellissodes. *Psyche*, 1908, pp. 122-124.

[4] Sur quelques Particularités curieuses du Rapprochement des Sexes chez certains Diptères. *Bull. Scientifique de la Belgique*, 7th Series, vol. XLV, pp. 1-14.

of reproductive behavior have been fairly constant since their origin."

MATERNAL BEHAVIOR

Baker and Turner (6) describe the oviposition of the green apple-aphis; Gruppy (39), of the syrphid flies; Harris (40), of the beetle *Bruchus*; Hayes (41), of the maize bill-bug; Knab (59), of *Dermatobia hominis*; Snyder (99), of the termites; Whitmarsh (117), of *Apateticus cynicus*; and Turner (111), of several Orthoptera.

Miller (66) describes, in detail, the method by which *Megastigmus spermotropus* slowly forces her ovipositor through the cone of the Douglas fir, lays her eggs and then withdraws the ovipositor.

Evans (29) informs us that, as a rule, the house-fly does not breed in garbage, although that is one of its favorite feeding places.

Rau (82) discovers that *Calliopsis nebraskaensis* Cfd., a solitary bee the nests of which form large colonies, keeps the entrance of its nest closed.

Pierce notes (81) that the weevil, *Polydesmus impressifrons*, deposits her eggs, in masses of from 20 to 80, under the loose bark of the willow, the poplar, the birch, the apple and the pear.

Urbahns (112) states that a parasitic fly, *Habrocytus medicagnis*, thrusts her ovipositor through the walls of the seed-pod of the alfalfa into the watery seed and lays her eggs upon the larva of a chalcid fly.

Smith (98) observed a parasitic Hymenopteran, *Perilampus hyalinus*, lay its eggs on the leaf of the oleander. The newly hatched larva is well supplied with hooks. It creeps about over the leaf, then stands erect, hooks itself on the first chrysopa larva that passes and bores into it.

In a series of seventy experiments, conducted on flies placed in solitary confinement as soon as they emerged, Hutchison (50) finds that the period of preoviposition of the house-fly varies from two and a half to twenty-three days, dependent upon the temperature, the humidity, and the kind and quality of the food.

McGregor (63) states that the privet mite oviposits about twenty eggs in either an abrasion, or a depression, or in old moulted skins.

Rau (83) describes in detail the nidification of the mud-wasps *Scleiphron caementarium*, *Chalybion caeruleum*, and *Trypoxylon*

albitarsis. He is convinced that Ashmead is in error when he claims that the last wasp mentioned uses the abandoned nests of the two former.

Turner (110) finds that an American false-spider, *Eremobates formicaria*, constructs her burrow much in the same manner as does the Indian *Galeodes*. In the lower portion of the burrow the milk-white eggs are deposited. The Indian form rests quietly among the eggs and later guards the newly hatched young from harm. The American form leaves her eggs unguarded, excavates a new burrow each night, and lays a second batch of eggs before the first has hatched.

The European wasp, *Methoca ichneumonides*, gives a tiger beetle larva an opportunity to seize her and then stings the larva and deposits her egg upon it. In an American form, *Methoca stygia*, studied by him, Williams (118) did not find any evidence of the wasp waiting for the larva to seize her. The wasp enters the burrow, stings the larva, lays an egg upon it, and then fills the burrow with sand.

Pellett (77) noticed that a paper wasp, *Polistes metricus*, Say, lays an egg almost daily upon the side of a cell, and that the mother spends most of her time feeding the young upon kneaded mosquitoes. The investigator captured mosquitoes and, after kneading them, gave them to the larva to eat. As long as the mother was living, she would remove the poorly kneaded mosquitoes, reknead them and eat them herself or else feed them to some other larva. In the absence of the female, he found it possible to raise the larvae upon these man-kneaded mosquitoes; but, the worker wasps thus raised would not nurse the remaining larvae.

According to Belsing (9), the pecan twig-girdler begins her egg-laying activities by girdling a twig. Although the branch is seldom cut through, yet its own weight usually soon severs it. On the twig the insect makes an incision, with her jaws, at the base of a leaf bud. The incision is excavated by the ovipositor, an egg deposited therein and the whole sealed with a black, gluey substance which is discharged by the ovipositor. With her mandibles, she then makes a number of small transverse incisions below the point where the egg has been laid. This causes the bark on drying to raise like a blister and not crush the egg.

Aquatic Lepidoptera are rare and almost no attention has been paid to the American forms. Recently Welch (116) has given a description of the morphology and behavior of two forms studied by him. In both species the mother lays the eggs upon submerged portions of water plants. Laboratory experiments demonstrate that in the case of *Nymphula macularis* Clem.: "(a) Eggs are invariably deposited at night. (b) Eggs are invariably placed about Donacia (chrysomelid beetle) egg holes when the latter are available. (c) Oviposition may extend over five successive nights. (d) One female may use several Donacia holes before oviposition ceases. (e) Maximum number of eggs laid by a single female was 617. (f) In the absence of Donacia holes or other similar punctures in the water-lily leaves, oviposition was usually delayed but ultimately resulted in the deposition of small egg masses on the lower sides of the leaves at the margins. Egg masses were deposited about artificial punctures and incisions of various sizes and shapes, the dimensions of which apparently had little to do with the selection."

HIBERNATION

Cosens (19) mentions the hibernation of the lady-bird beetles of Canada.

Coad (15) finds that the pupa of the wild-cotton weevil hibernates in the bolls of *Thurbergia.*

Osborn (70) gives a list of the leaf hoppers that hibernate in Maine.

Sell (94) could find no experimental evidence that the 12-spotted cucumber beetle hibernates.

Our literature on the hibernation of flies has been augmented by articles by Ashworth (4) and Dove (25). The latter investigator finds that, in Texas, the pupae and the larvae of the house-fly overwinter in naturally accumulated manure piles. Throughout the mild winter weather adults occasionally emerge from those piles to which fresh manure is continually added. In the spring large numbers emerge.

ECOLOGY

In a paper too well filled with good things to permit of an adequate review in the limited space of this article, Adams (1) discusses the ecology of prairie and forest invertebrates.

Patch (74) contends that the most important problem in the ecology of any aphid is, " Does it migrate ?"

In his investigations of aquatic Lepidoptera Welch (116) studied both *Nymphala macularis* Clem. and *Nymphala iccualis* Wlk.; but, most of his time was devoted to the former. The larva cannot swim; its sole method of locomotion is by crawling. In both species case-making is a constant larval activity. The case is constructed out of bits of the leaves of the food-plants. This case serves as a protection and as a float.

LETISIMULATION

It is well known that the coccinellid beetle *Epilachna borealis*, when disturbed, folds its antennae and legs against the body, ejects small drops of liquid from its femoral articulations and feigns death. What is the nature of this excretion and how is it expelled so quickly ? McIndoo (64) has demonstrated that this " reflex bleeding " is a true reflex, that the fluid is secreted by hyperdermal glands, that it is ejected through groups of pores situated on and adjacent to the articular membrane, and that its ejection is accomplished by putting the gland cells under high blood pressure.

DuPorte's (27) description of the death-feigning of *Tychius picirostris* harmonizes with the accounts of the letisimulations of other invertebrates as related by several recent investigators. (1) There is much individuality. (2) There is no relation between the intensity of the shock and the duration of the feint. (3) It is impossible to prolong the feint indefinitely by means of repeated stimulations. (4) The animal may be much mutilated without being aroused from the feint. He thinks that the physico-chemical reaction responsible for the manifestation of the death feint is of the same nature as that which calls forth the thigmotactic responses of many insects and other animals and such plants as *Mimosa*. The reaction is segmental and not controlled by the supra-oesophageal ganglion.

MIGRATIONS

Osburn (69) has a short note on the migration of dragon-flies and Barber (7), one on the migration of Myrapods.

About five years ago, Zetek* devised a method of marking

* Determination of the Flight of Mosquitoes. *Ann. Antom. Soc. of Amer.*, 1912, vol. VI, pp. 5-21.

insects with an aniline spray and a means of diffusing it out from captured individuals. Parker (73) makes use of this method in studying the dispersal of the house-fly in cities: 1,056 flies were captured at from 50 to 3,500 yards from their breeding place, thus demonstrating what wide range of territory may be infested from a single infested locality.

Although there have been some dissenting voices, the large swarms of monarch butterflies and of certain dragon-flies seen flying southward in the fall and northward in the spring have been considered seasonal migrations; but, in the past, there has been no such intensive study of insect migrations as has been devoted to bird migrations. Partly as a result of observations made on our Atlantic coast, partly due to extensive reading, Shannon (97) concludes that dragon-flies, the monarch butterfly, the great sulphur and perhaps other insects migrate in certain definite routes which coincide with those followed by migrating birds. These routes seem to be a function of the physiographic features of the country. In the U. S. A. he maps four routes: (1) Extending along the Atlantic coast from Canada to the Gulf of Mexico. (2) Extending along the northern shores of Lake Ontario and Lake Erie and then down the Mississippi Valley. (3) Extending along the western shore of Lake Michigan and then down the Mississippi Valley. (4) Extending along the western shore of Lake Superior and then south along the Great Plains.

MISCELLANEOUS ACTIVITIES

Disease Spreading Activities.—Articles on the relation of insects to the spread of diseases have appeared by Brittain (11), Cummins (21), Fitzsimmons (31), Hindle (46), King (57), Payne (76), Roberg (87), Studhalter (102), Townsend (106, 107, 108), and Zetek (120).

Locomotion.—Amans (3) describes the method of flight of the cicadas and King (56) of the locomotion of *Pterodontia flavipes.*

Parasitism.—Parasites have been discussed by Good (37), Graham-Smith (38), Packard (71), Phil and Nellie Rau (83), and Weidman (115).

Phosphorescence.—Notes on the synchronous flashing of fireflies have been published by Allard (2) and Morse (65).

Respiration.—d'Orchymont (68) describes in detail the methods of respiration of certain aquatic insects.

Pollination.—Nägeli, Bonnier, Schroeter, Mrs. Soth and others believe that there is a scarcity of insect visitors to flowers above the timber line. Kenoyer's (55) studies lend themselves to a different interpretation. "Selecting comparable weather and excluding the honey-bee, which does not live at high altitudes, it seems to me that the flowers above the timber line are as much visited by insects as those of lower altitudes, and I have no reason to suppose that they are less dependent for pollination upon their insect visitors." His view harmonizes with those of Muller and L. H. Pammel.

Temperature Effects.—Back and Pemberton (5), Phillips and Demuth (78), and Pierce (80), have discussed the effects of temperature upon insects.

SLEEPING BEHAVIOR

In the past very little attention has been paid to the sleep of insects. The Raus (84), by making a careful field study of the sleep of more than a hundred species have partially remedied this defect in our literature. Lack of space prevents an adequate consideration of the contents of the article. It is thought that the following extract from their summary will prove of interest: "The sleep of an organism signifies more than a mere pause in its activity while darkness covers it; while we have not in the present paper touched on the physiological phenomena of their sleep, we have found many interesting associations of this with other activities of the insects. For instance, it is of marked biological interest that a few species certainly seem to choose protectively colored situations, and others select sites which are in various ways protective; that some which are solitary by day are gregarious by night, that some insects sleep with all the regularity of a theoretical modern infant, while others of a more unsystematic life snatch a wink when they can. . . . Vegetable feeders are more frequently regular sleepers, while carnivorous species are irregular. . . . The sleep of animals in immature stages, the larval, pupal or even egg stage, is something untouched upon."

MEMORY AND RECOGNITION

Sell (94) states that the homing of the 12-spotted cucumber beetle is not influenced by a homing instinct.

Rau (82) discovered a leaf-cutting bee, *Megachile brevis*, carrying bits of leaves to a burrow on the southern end of one of the ties of a railroad track. A passing train disturbed her and she seemed to lose her bearings. She searched tie after tie, but always on the southern end only. This caused Rau to conclude that she used the ties as land-marks.

In his studies of the breeding habits of Orthoptera, Turner (111) states that excitement in the presence of the opposite sex is not alone an indication of sex discrimination. "In this state of excitement males will seize other males, members of other species, or even a stick to which the abdomen of a female has been attached. On the other hand there is an entire lack of anything that would indicate excitement in some forms."

TECHNIQUE

Packard (71) discusses methods of rearing the following parasites of the Hessian fly: *Micromelus subapterus* Riley, *Eupelmus allynii* French, and *Merisus destructor* Say.

Dow (26) describes a method of making plaster casts of insect burrows that will interest all students of our subterranean fauna. Mix equal parts of plaster of Paris and water and, by the aid of a paper funnel, pour immediately into the burrow. Three ounces of the mixture are required for *Cincindela*, one and a half for the pepo spider and seven to nine ounces for *Colletes*. It is best to make the cast one week-end and to excavate it the next. In excavating, dig a pit alongside, one foot from the vertical and deeper than the bottom of the burrow. Then, with a stout knife, begin at the bottom and work the dirt away from the cast. If the bottom is not freed first the tube will break. He finds that the species of the tiger beetle can be differentiated by means of their burrows.

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LITERATURE FOR 1916 ON ANTS AND MYRMECOPHILS

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The literature on ant behavior for the year 1916 shows a rather marked predominance in the number of economic papers. In a way this is encouraging for it indicates that the students of economic entomology are tending to place more emphasis upon the general biology of the forms under investigation. Much of the matter in the following pages will be found to have been taken from papers whose point of view is in the main economic.

ECONOMIC RELATIONSHIPS

According to Marlatt (13) the ants that are house pests in North America are, in practically all cases, of tropical origin. Still further, nearly all the ants that have been introduced into North America from Europe and South America, whether house pests or not, are tropical species. In their tropical climate these ants are usually outdoor species but in the temperate regions can usually exist only in houses, green-houses, etc. Most of these ants are annoying rather than harmful, but some of them and especially the Argentine ant (*Iridomyrmex humilis*) are first class pests. Marlatt classifies our ant pests upon a basis of their origin, as follows: Tropical old world ants, 12 species; ants from the new world tropics, 5 species; native North American ants of temperate regions, 2 species.

Of the imported ants whose behavior makes them first class pests, the Argentine ant has, during the past year, received much attention. Donisthorpe (6) states that this species is becoming a serious pest in England. Barber (1) has made a rather extended study of the habits of this ant and speaks of it as being one of the " worst of pests." In the house, he says, it eats everything. The temperature of ice boxes has no deterrent effect and it invades every room in the house. In one case a young baby was attacked

with serious results. This ant (1) is also the bane of nurserymen, since it protects aphids in great numbers. The ants build mud shelters over the aphids and see that the young lice are placed on the tenderest shoots.

The summer nest of the Argentine ant is located anywhere (1) but in the autumn the summer colonies tend to concentrate into larger colonies. They cannot stand the wet, freezing conditions of winter in the open, but seek a warm, dry place in which to hibernate. Thus they may frequently be found spending the winter in manure piles or other heat generating rubbish. When these winter colonies break up in the spring, the ants are particularly annoying, as they spread out, looking for summer homes.

In an artificial formicary (1) a queen Argentine ant lays from 3-30 eggs daily. The eggs are immediately taken by the workers and piled with others. Being slightly sticky they cling together and are handled in clumps.

Further ant pests, which may but await importation from the tropics, are indicated in the papers by Mann (12) and Crawley (5). Crawley in publishing notes on the ants from British Guiana, lists a number of species that would seem to be potential house pests. *Solenopsis corticalis* lives exclusively in habitations and is fond of all food stuffs. This species is a severe pest in entomological laboratories. It possesses a powerful sting. *Tetramorium guineense* is a serious pest in cane fields. It stings readily and painfully, and is sometimes so numerous that it is next to impossible for the cane cutters to work in the fields. *Atta cephalotes* kills all kinds of cultivated plants and *Paraponera clavata* possesses a sting that frequently brings on a fever. To give the ants of Guiana full credit one should mention *Ectatomma quadridens*, which lives in the cultivated areas; this species is beneficial in the cane fields as it carries off the larvae of a moth and a weevil borer. It also destroys the egg clusters of the moth. Mann (12) records an instance of beneficial behavior upon the part of *Eciton praedator* which he saw emerging from a commissary building in countless numbers and carrying an "incredible number of insects, mostly cockroaches." Mann, however, lists a number of other species that must possess serious detrimental potentialities should they once gain foothold in temperate regions. Snyder (17) has continued

his investigations into the biology of our North American termites and has added many facts of interest to our knowledge of these insects. He has found that white ants occasionally injure living trees and shrubs, in the southern part of the United States. In Florida, they have at times done considerable damage to the newly planted groves of orange trees by eating away the bark and gradually girdling the tree. Similar damage has been reported for apple, peach, pear, cherry, plum, apricot and lemon. In California, pecan, chestnut and walnut are attacked as well. In other parts of the United States a great variety of shade trees are attacked. Snyder says, that all such damage is more likely to occur in new soil or recently cleared woodland, especially in the latter, if the stumps are still standing.

In the south, termites also occasionally injure the stems and roots of a great variety of healthy field crops, both grain and truck; they attack corn, cotton, sugar cane, rice, grasses, potatoes, and garden vegetables. In the prairie regions of Texas and Arizona there is a tube forming termite that lives in the ground and feeds on the roots of the grass. This species is often found under and in, dry cow dung. It has been known to destroy the vegetation over large areas of grazing land.

DISPERSAL OF ANTS

The first colony of the Argentine ant reported for the United States was found in New Orleans in 1891. At the present time there are myriads of colonies covering 1000 square miles of territory and extending from Houston, Texas, to Wilmington, N. C., and from Nashville, Tenn., to the mouth of the Mississippi River (1). Food scarcity hastens the spread of the species. The normal advance under ordinary conditions is from 300-400 feet a year, but rapid dispersal over large areas may take place at times of heavy floods, as the ants will ride in floating rubbish of all sorts. They do not drown easily and when the rising water floods their nests they frequently cluster together to form a compact ball. The immature stages form the center of the ball with the queens and the workers on the outside. As the ball enlarges by the addition of other workers struggling alone in the water, it slowly revolves and thus the mass is aerated. This aeration is automatic and continuous, for the ants on the under side of the ball are constantly striving to get out of the

water by crawling to the top. Such balls may attain a diameter of 6-8 inches and may float about for hours in still water. Upon coming in contact with a solid substance the ball breaks up and the ants crawl out. If coal-oil is poured on the water the ball breaks up and the ants soon die.

Wheeler (25) cites an interesting case of dispersal of a tropical ant (*Pheidole feregrina*, New Sp.), a small colony of which was conveyed in a floating log from the main coast of Brazil to San Sebastian Island, which is about forty miles off shore. Wheeler points out, in this connection, that it is not necessary that an entire colony should be transported to ensure the widening of the distribution of the species; one fertilized queen would be sufficient. Dr. Herman von Ihering, who has been experimenting on this phase of ant dispersal, is quoted by Wheeler as saying, that his experiments with bamboo and other kinds of wood, containing ant colonies, have demonstrated that the ants which he used are decidedly resistant to submersion, provided the nest entrances are closed.

Wheeler (20), while going over the Pergande collection of ants, found a series of workers of the Indian ant *Triglyphothrix striatidens*. These workers were collected in Louisiana, where the ant must have been introduced quite recently. The original home of this ant is Southern Asia and Wheeler's is the first record of its occurrence in the United States. The species, according to Wheeler, is now pretty well spread over the tropics. Its introduction into other parts of this country is but a matter of time, if indeed not already accomplished.

Barber (1) states that the greatest means of dispersal of the Argentine ant in the United States is by steamboats and railroads. They will, he says, ride in lumber, fruit, vegetables, etc. For this reason infestation usually starts around the wholesale grocery and commission merchant houses.

CONTROL OF ANT PESTS

The study of the control of any pest is primarily a study in animal behavior. The study of the control of ant pests consists largely, in the discovery of substances that will either repel or poison them. The literature on this subject should, therefore, furnish one with data concerning ant sense organs, their location, sensitivity, etc. However, this rather purely biological

side of the problem has not, as yet, received much attention at the hands of the economic entomologist, who for the most part, finds that he must look for results rather than causes and explanations.

Gibson (9) states that one or two applications of sodium fluoride, dusted in cracks, etc., will cause the species *Camponotus pennsylvanica* and *Cremastogaster lineolata* to leave an infested house. The author believes, but has not demonstrated, that the same remedy will work for other species as well. Horton (10) gives several recipes for anti-ant bands. Sulphur and $HgCl_2$ are the primary ingredients recommended and it is stated that ants can be kept out of trees and cupboards for from 2-5 months with one application. Marlatt (13) says sticky bands do not prevent the Argentine ant ascending trees, for it at once builds a bridge of dirt across the band. The Argentine ant will avoid a quick poison and is repelled to some extent by it. Ant bands containing $HgCl_2$ act as a repellent and are recommended.

RELATION OF ANTS TO OTHER SPECIES AND TO OTHER INSECTS

Myrmecophily.—On April 19, 1915, Donisthorpe (7) captured a specimen of the beetle *Myrmedonia limbata*, which he found running with a number of *Lasius nigra* workers, on the sand bank in which the ant's nest was located. Donisthorpe also records collecting a spider (*Micryphantis beatus*) that looks so nearly like the workers of *Tapinoma erraticum* with which it was running about, that he at first took it to be an ant. This same author has a nest of *L. umbratus* in which an individual of the beetle *Amphotis marginata* has lived for one and one-half years. He records, also, data concerning the behavior of *Myrmica scabrinoides* toward the lepidopterous larva *Lycaena arion*. This larva it appears is not molested by the ants although it eats their eggs and larvae.

Crawley (4) attempts to show that the claviger beetle *C. testaceus* is more strongly attracted toward the queens of *Lasius umbratus* than to those of *L. flavus*, which latter is the normal host. He says, that when he placed a number of the beetles into nests containing *L. umbratus* queens, they clung to the queens and did not seem to change their resting place for weeks. He thinks that it is probable that the parasitic queens (*L. um-*

bratus, *L. fuliginosus* and others) have a body secretion which renders them attractive to the myrmecophils and to other species of ants.

Donisthorpe (7) does not agree with Crawley in believing that the claviger beetles are attracted more strongly by the parasitic queens than by the queen of their normal host; he thinks rather, that they cling without preference to the gaster of the queen of any of the species with which they are associated.

Ants and Other Insects.—The relations of ants to other insects, that are not, strictly speaking, myrmecophils, furnishes a wide field for investigation. The literature for 1916 contains many new data bearing on this aspect of ant behavior. Theobald (18) describes a new genus of aphids taken by Crawley in the nests of various species of *Lasius*. Smith (14) records the following species as attending aphids and other insects in South Carolina. *Iridomyrmex pruinosus* he found attending the " green bugs," *Toxoptera graminum;* this aphis was also attended by the ant *Dorymyrmex pyramicus*. *Prenolepis imparis* attends the black elder aphis, *Aphis sambucifolia*, and also the cottony cushion scale, *Icerya purchasi*. *Cremastogaster lineolata* and *Prenolepis impari* attend the scale insect on the pine (Toumeyella pini).

An interesting piece of behavior upon the part of a tiger beetle and an ant is recorded by McAtee (11). This author saw the beetle standing motionless in a road with the ant running all over the surface of its body. The beetle, which proved to be *Cicindela unipunctata*, ran actively when the observer attempted to catch it. The ant was identified as *Formica fusca*, var. *subsericea*. Mann (12) in his discussion of the ants of Brazil says that *Platythyrea meinerti* probably lives in termites nests but does not give any information as to whether or not the ants occupy the same galleries with the termites. Crawley (5) also records an ant (*Dolichoderus debilis*) that makes its formicary in the nest of a termite. Termites were still living in the nest but whether or not they mingled with the ants is not stated. Crawley reports that the common leaf cutting ant (*Atta cephalotes*) of British Guiana is accompanied by a muscid fly that laps up an excretion from the tip of the ant's abdomen.

Social Relations of Ants.—The Argentine ant (1) will not tolerate any other species of ant but drives them out before it. Among its own kind, however, it is extremely social and workers

from widely separated colonies mix readily. There are usually several queens in any small nest and they live together amicably. In the winter nests there may be several hundred queens and countless workers and immature stages. *Eciton hamatum*, a common Brazilian ant (12), lives largely upon other ants. It attacks particularly *Dolichoderus lugens*, which latter species secretes from the anal gland a large drop of yellow liquid which Mann takes to be protective. Another case of predaceous relationship among ants is suggested by Donisthorpe (6), who describes a new species of *Epitritus* from Hawaii. He states that this species, which he calls *wheeleri*, probably accompanies other ant species and preys upon their brood stages.

Donisthorpe (7) had a colony of *Leptothorax nylanderi* into which, as food, he introduced some worker pupae of *Myrmica scabrinoides*. Some of the pupae were eaten but others were not harmed and the adults emerged in due time. Most of the Myrmica workers were killed at once, but for some reason one was allowed to go unharmed. This individual lived in the Leptothorax colony for three months, when it died an apparently natural death.

Up to the year 1915, according to Donisthorpe, there was only one instance on record where queen ants have been reared from eggs laid in captivity. For five years Donisthorpe had kept a colony of *Myrmecina gramnicola* but no queens were produced. On July 1, 1915, however, three winged females appeared from pupae, which must have been reared in the captive nest. By July 10, fifty winged females were present and many others appeared later. Only one male was seen. No mating was observed but by the end of August many of the females were removing their wings. On September 16, the male was seen flying about in a very excited way in the nest; the next day it was dead.

The winged females helped to carry about the larvae, to kill and cut up flies, and in general behaved as workers. The last one removed her wings December 15 and all the deälated females continued to behave as workers. As to whether or not they will lay eggs remains to be seen. The only explanation which Donisthorpe suggests for the appearance of the sexual forms is that he had fed the colony an unusually large amount of animal food.

Wheeler has stated in previous papers, that if the wings of a virgin ant queen be removed, she will behave like a fertilized queen. This does not seem to have been the case with Donisthorpe's queens which, as just related, behaved like workers after removing their own wings. Crawley has maintained that deälated virgin queens of the genus *Lasius* do not behave as though fertilized. To test this question for *Lasius*, Donisthorpe (7) on September 3rd, 1915, introduced into a queenless *umbratus* colony a virgin *fuliginosus*, from which he had removed the wings. The queen ran around among the *umbratus* workers tapping them with her antennae and was accepted by them. She was cleaned and given the attention due a queen from her workers. On September 7 the nest was left in the sun and some of the workers began pulling the queen about; when the nest was placed in a cool situation the queen was again accepted and on December 19 had not again been attacked. Whether or not a deälated virgin female will act as a queen, probably depends upon more than mere loss of wings. The receptivity of the colony in which she finds herself is undoubtedly important. Crawley (5) points out that the tropical ant *Tetramormimum guineense* has ergatoid females which are only slightly larger than the workers and run about with them.

ORIENTATION OF ANTS

Brun (3) believes he has shown that the higher ants orient by using large distant land-marks; he thinks the lower ants do this also but to a smaller extent. The higher ants, he finds, can complete the hypothenuse of a triangle, even from a considerable distance. This, he says, is not due to kinaesthesia or to a sense of angles but to the utilization of a visibly distant landmark. These same species show some measure of local memory and Brun believes that the recognition of "known localities" is probably a function of a "topochemical" sense, while the choice of direction depends upon memory.

Orientation after transport, according to Brun, depends on the localization of illumination by the compound eyes and is not exhibited if the illumination is bipolar. Ants cannot associate a complex succession of diverse positions of the median plane of the body, and except within narrow limits, there does not seem to be much kinaesthetic sense of attitudes. There is

no static sense. Ants are, however, sensitive to gravity and utilize the hints given by the slope of the route. There is (3) no sense of memory of direction as such, for there is no power of orientation except under the influence of the various stimuli mentioned above.

Wheeler (21) noted that on a certain raid made by the Amazon ant (*Polyergus breivceps*) the raiders which were fully 200 feet from their own nest, returned at once in the right direction, with their plunder, although for forty feet the path taken was entirely different from the one over which they had come.

NOISES MADE BY ANTS

Ectatoma quadridens, a British Guiana ant (5), makes a squeaking sound when it is captured. *Daceton armigerum*, another tropical ant, when captured and placed in alcohol emits from time to time a sharp click. *Azteca schimperi* lives in large carton nests built on the r nks of trees (mango). When disturbed the ants swarm out, making an audible rustling noise. *Paraponera clavata* (15) when disturbed comes rushing out making a stridulating noise. Horton (10) says that when the $HgCl^2$ ant bands are placed around the tree trunks many ants are frequently confined above them in the trees. He has seen these imprisoned ants congregate just above the bands and in some way attract large numbers of free ants which collect on the lower side of the band; there they become so excited that they make desperate attempts to cross the deadly area. The author suggests that stridulations by the confined ants attract and excite the others.

SWARMING OF ANTS

Mating.—Gaige (8) records the following dates for the swarming of ants on White Fish Point, Mich.: *Cremastogaster lineolata*, August 27, by hundreds; *Myrmica scabrinoides*, August 10; *Formica sanguinea*, July 8-9; many more females than males. *Camponotus herculanius*, colonies contain winged males and females all summer and swarming occurs from May 14 to August 14. Smith (14) saw *Prenolepis imparis* swarming, March 19, in South Carolina. Wheeler (21) in watching the Amazon ant go out on its slave raids in late July noted that one day a partial marriage flight took place at the same time. This was

in the Sierras in Southern California. The author calls attention to the fact that Emery has shown that the fecundated and deälated female of *Polyergus* founds the colony by entering a *Fusca* nest, killing the queen and taking her place. Wheeler suggests that perhaps the *Polyergus* queen stays behind after the raid. Wheeler has made a very interesting observation on the formation of the *Polyergus* colony in that on July 24 he found an incipient colony of this species which was made up of an ergatoid queen, about a dozen workers and two dozen slaves. The ergatoid female is wingless but apparently can function as a queen. Dissection shows that she has the same organs as the winged queen form. If she is not fertilized, only male progeny will be produced but she may be fertilized, either inside or outside the nest.

Wheeler (19) publishes the first full account of the swarming of the Australian bull-dog ant, *Myrmecia sanguinea*. During the last week of November, he states, there were no winged males or females in the nests of this ant, but plenty of larvae and small numbers of worker pupae. The lack of winged forms was surprising (19) as the sexual forms of most of the ants of New South Wales are to be found in the nests in late October and early November. It was found later, that the sexual forms of the bull-dog ant do not mature till January. They were observed to swarm on January 30 after some very hot, stormy weather. The winged forms were present by thousands and were flying and crawling about in the bushes where copulation was taking place. There were apparently hundreds of males to one female; result, every female was surrounded by a mass of males as big as one's fist. The balls of ants were continually breaking apart and new ones were forming. These ants, which ordinarily are exceedingly pugnacious and can clearly discern objects several feet away, paid no attention to the observer. A similar flight of this ant is described as taking place in early April, in South Australia.

Wheeler (19) points out that these observations prove that the species of the *Ponerine* genus *Myrmecia* celebrate a regular marriage flight like all the ants of the other taxonomic subfamilies, except the species with wingless males and females. The flights occur in January in Northern New South Wales and a few months later, farther south, in the colder parts of Aus-

tralia. Wheeler has observed that the fertilized females of this species lose their wings and found a colony just as do the higher types of ants.

Snyder (16) says that when termites swarm for the mating flight they do not fly more than 75-100 feet from the original colony. It is of interest to note that with the termites copulation between the royal pair is repeated at irregular intervals over several years. There is apparently no adaptation, as in the ants, for keeping the sperm alive indefinitely in the queen's body.

Swarming for slave raids.—Wheeler (21) camped during the summer of 1915 near Lake Tahoe in the Sierras in California. His camp was situated at an altitude of from 6,000 to 7,000 feet. During the summer he had the opportunity of witnessing several of the slave raids of the western Amazon ant (*Polyergus breviceps*). The slave was always an "ill-defined" variety of *Formica fusca.* Wheeler found that these raids always took place between 3:00 P. M. and 5:30 P. M., on warm days, during the latter part of July. The *Formica fusca* colonies usually tried to resist the Amazons by plugging up the nest entrances with pellets of earth; in one case the *fusca* ants fought so valiantly that the battle raged for 30 minutes and until most of the defenders had been killed. Before starting on the raid, the *breviceps* ants came out of their holes and congregated about the openings. Then at some indistinguishable signal they usually hurried off greatly excited. Winged females were seen to accompany the workers and in some cases they entered the *Fusca* nest but usually did not return with the pupa-laden workers.

On one raid part of the army plundered a small nest and returned home with the plunder, while most of the army went on. In one attack where the *Fusca* ants defended vigorously, part of the Amazon ants fought while others kept digging at the earthen barricade which the *Fusca* ants had thrown up. On this particular raid several deälated females were seen to return with the workers but they carried no plunder.

On July 30 the ants made no raid and the weather was cloudy and much colder than on previous days. A number of winged males were constantly coming to the opening of the nest but most of them were dragged violently back by the *Fusca* slaves. A few escaped and flew away. Wheeler says that the slaves

were very active at the entrances to the nest and seemed to be keeping the worker Amazons from making a sortie.

Wheeler points out that the raids here described took place about two hours later than those recorded for the same and other species in Colorado, Illinois, Pennsylvania, and New York. He is inclined to believe that temperature and humidity in some way regulate the time and day of the raid. The optimum temperature for such raids he thinks is near 70 to 75 degrees F. Wheeler states that future descriptions of Amazon expeditions should be accompanied by accurate temperature, barometric and humidity readings. The writer of this review hopes the future investigators will take this suggestion of Wheeler's very much to heart. Furthermore, the procedure which Wheeler suggests should not be limited to slave raids of Amazon ants. Every student of animal behavior should keep an accurate record of the environmental conditions under which the behavior, which he records, took place. This suggestion is particularly applicable to students and observers of insect behavior. Our entomological journals are filled with new and interesting records of observations on insect behavior but in practically no case has the observer taken the time to record for us, the temperature, the humidity, the rate of evaporation or any other of the environmental factors that must have played such a large part in determining the reactions which he records. One need not feel that the recording of such factors makes him an advocate of the mechanistic hypothesis, yet I am afraid that some feeling of this kind does prevent certain entomologists from taking such records seriously. Whether or not organisms are mechanisms does not in the least alter the fact, which would seem to be obvious, but which has also been demonstrated again and again experimentally, namely, that animals in their natural environments are continually reacting to, and in many cases are largely controlled by the stimuli, which impinge upon their receptors from the surrounding environment. Experiment has also shown quite clearly that temperature, light, and rate of evaporation are especially important in the influence which they exert upon the reactions of animals. No observer should consider his field outfit complete until he has added to it a thermometer, an atmometer and a photometer. None of these instruments is complicated or bulky and all can be carried into the field without

inconvenience. It is to be hoped that they will come into immediate and general use.

GENERAL FACTS CONCERNING ANT BEHAVIOR

Atta laevigata, a Brazilian ant (5), cuts up leaves and carries them into its nest only at night. It begins work after sundown and quits just before dawn. *Atta cephalotes*, the common leaf-cutting ant, also works only at night, except for a few small forms which may carry sand about during the day. Light seems to play an important part in the lives of these species. Ants in general seem to be very sensitive to light and moisture. Mann (12) records that *Eciton filosum* prefers to travel under ground and when it comes to an impassable barrier constructs an earthen tunnel over it. This behavior is very much like that of the termites which are very negative to light and require constant access to moisture. Snyder (16) says that the center of activity in termite colonies is governed to a considerable extent by the wetness of the season. In moist springs the outlying galleries are teeming with life while in the summer these galleries are too dry to be used. In arid regions termites burrow deep into the ground all the year round, as they do in summer only in moister localities. In temperate regions they enter the ground in October and November and do not emerge till February or March. Termites can work in dry, hard wood and in other dry substances far from the ground, provided there is access somewhere to damp earth. They use a mixture of moist earth and finely digested excreted wood in creating more favorable conditions of moisture and shelter, while extending their galleries. They pass over concrete and brick by means of small shelter sheds which they construct across the obstacle. In the Southwest (Texas and Arizona) there is a species of termite that lives in the grass-lands and is able to live on the grass above the ground by covering the stems with earthen tubes.

Concerning the general habits of termites, Snyder (16) says that in North America they do not construct permanent nests but change their location from time to time. An average colony contains several thousand individuals while an old, long established colony, may be inhabited by tens of thousands. The increase in numbers in a young colony is slow. Snyder further states that termites usually follow the grain when working

in solid wood. The tunnels of their nests therefore run parallel to the grain of the wood.

Among other interesting notes on the ants of Brazil, Mann (12) describes the habits of the ant *Pseudomyrma arboris*, which he says lives in trees of the genus *Triplaris*. The natives say that this species never lives anywhere else and never lives on any but the live tree. Also, in all live trees of this genus, the ant is to be found living in the hollow parts of the stem. That the ants protect the trees is easily demonstrated, for they are very pugnacious and possess a painful sting. Whether or not they receive any advantage from the tree, other than that of being furnished a place to nest, is not determined. Crawley (5) describes the ant *Cryptocerus minutis* as being very sluggish and states that it will remain absolutely motionless on a leaf for hours at a time. Smith (15) saw, on April 15, 1916, *Trachymyrmex septentrionalis* out for the first time that spring, in South Carolina. The workers, he says, were taking apple petals into the nest for the purpose of growing fungus on them. Beebe (2) collected and examined four square feet of tropical jungle ground stratum and found 1,000 species of animals therein. Ants made up 30 per cent of this total. Termites were also abundant. Two new genera of ants testify to the unexplored state of this part of the jungle. Most of the ants were found below the surface layer; in fact this middle layer contained four-fifths of all the animals found. The ants were living in small colonies in the semi-decayed twigs. The colonies seem to be complete though there were only 5-15 individuals in any given colony.

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LITERATURE FOR 1916 ON THE BEHAVIOR OF VERTEBRATES

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SOUND

Mammals.—The animal literature this year reflects the popular interest in other psychological fields in that the papers are chiefly devoted to the learning process. There are only two articles to report on sound. One is a timely article by Reuter (22a) which discusses the effect of heavy firing upon animals. He says: "Soon after the beginning of hostilities game began to migrate into Luxemburg, Switzerland, and those parts of France and Belgium which were distant from the warfare. The first to go were the wild boar, badger and bear, followed by the roebuck and red deer. The hare, noted for its timidity, continued in its old territory. The larger birds, grouse, pheasant, sea-eagle and wild duck were driven away, but the song birds continued to build their nests and sing as usual. The house dog seems more resistant to the noise of detonation than do other dogs. But the thoroughbred and halfbred horse is more sensitive than the common horse and the celebrated Russian horses than the German war horses, drawn from all sources, which quickly become inured to the noise of battle."

Peterson (21a) suggests that if Hunter's results prove to be correct, if the white rat is deaf to tones and not to noise, the animal should furnish us with valuable data toward settling the question as to how the ear analyzes the complex vibrations of the air waves. For there must be some anatomical condition which is responsible for the lack of sympathetic resonance in the cochlea of the white rat.

CUTANEOUS SENSITIVITY

Fishes and Amphibians.—The existence of a common chemical sense is still a subject for discussion. Crozier (7) argues for such existence as against Coghill, who thought that the reac-

tions were caused by the use of a high concentration of acids which disrupted the permanently embryonic cells of the germinative layer in the skin of amphibians and fishes. He bases his conclusions upon experimental behavioristic evidence and micro-chemical studies.

Sayle studied (24) the reactions of Necturus to stimuli through the skin. She found it everywhere sensitive to tactile and chemical stimulation, although some parts were more sensitive than others. When any part was fatigued for a given chemical it rarely responded to tactile stimulation although it usually reacted to other chemicals. Both the eyes and skin are photoreceptors and the stimulation of either brings about a negative reaction.

VISION

Birds—and mammals.—Two years ago, it may be remembered, Johnson published the first of an admirable series of articles on visual discrimination in vertebrates. These are followed, this year, by three others (13). The previous experiments determined the width of striae in a field which could be distinguished as striae at a given distance under experimental control. Paper III reports an attempt with the same animals, a monkey and two chicks, to ascertain what differences in the width of two systems of striae, both of which have proved distinguishable, are necessary to effect discrimination. He found that the monkey could distinguish differences in width of striae of less than 3%. This is quite comparable with human ability but roughly is ten times greater than the ability shown by the chick 2. In the next experiment the differences in the direction of the striae furnished the basis for discrimination. The monkey's difference threshold for direction of elements of a pattern lay between 2° and 5°, the chick's between 25° and 40°. The relative improvement brought about by training was much greater in the monkey than in the chick. The third paper gives a carefully controlled demonstration of the dog's deficiency in detail vision and ascribes these factual results to the relative insensitivity of the retina to the differences of distribution of brightness over it.

The spectrum of the domestic fowl is the subject of a study by Lashley (16), who says: "The present paper offers further evidence for the existence of color vision in the fowl, in the

form of data upon the relative stimulating effect of different wave lengths upon the light and dark adapted eye, the ability of the fowl to react upon the basis of wave lengths, and the appearance of relatively abrupt changes in the stimulating value of different parts of the spectrum." The Yerkes-Watson color apparatus, with slight modifications, was used and the experiments were subject to a high degree of control.

In a study on the spectral sensitivity of birds Watson (28) says that the limit of the chick's spectrum at the red end lies probably between $\lambda = 7000$ and $\lambda = 7150$; at the violet end, between $\lambda = 3950$ and $\lambda = 4050$. This range is similar to that of man except in the extreme red end. The range of spectral sensitivity in the homing pigeon lies approximately between $\lambda = 4200$ and $\lambda = 7100$.

REFLEX AND RHYTHMIC ACTIVITIES

General.—The conditioned reflex is urged by Watson (26) as a method *par excellence* in psychology. He describes the technique and discusses various phases of the problem, persistence, reinforcement, inhibition, etc., and concludes by sketching ways in which the reflex may be used to obtain differential reactions. Craig (6) would like to know whether we find in animals anything like the synchronism of rhythm exhibited by men as they march or dance or keep step to music. Such a correlation of activities involves a conceptual awareness of the relation of one's own action to that of others. But, the author asks, may not animals have some innate mechanism which would bring them into synchronism with some external rhythm. He examines the evidence for many forms and says that if we reject (1) the slow rhythm due to day and night or seasonal changes and (2) cases in which there is bodily contact with the other rhythmical object as canary and perch or spider and web the case seems good only for the cricket chirping, "And even in that case it is still somewhat in doubt whether their simultaneity is accidental or due to the influence of environment or due to a lock and key adaptation by which one cricket stimulates the other."

Mammals.—The reflex by means of which cats in falling always turn in the air and land on their feet was studied experimentally by Muller and Weed (19). They found that the normal cats

which they tested could complete the turn within a one foot fall and some even in six inches. Blindfolded animals did this also but not quite so accurately. They destroyed the semicircular canals in a few animals and these turned also but not quite so perfectly and they required a greater distance. Animals in which there was unilateral destruction turned and landed on their feet, but the turn was characteristic, i.e., always away from the lesion. When these animals with one or both canals destroyed were blindfolded the reflex failed. Only a few with one side destroyed succeeded in turning. Ablation of the motor cortex bi- or unilaterally did not abolish it. It occurred even when blindfolded. Decerebration abolished it. The authors conclude that the reflex depends upon excitation derived from the eyes or the semicircular canals, but their evidence was non-conclusive either for or against Sherrington's theory that the muscles predominantly affected are those which antagonize gravity.

Amphibians.—Howat (12) studied the effect of nicotine on the skin reflexes of frogs. She found that certain spots in the frog's skin differ not only in irritability and reflex action but also in susceptibility to the influence of nicotine. The skin reflexes were affected by much smaller quantities of nicotine than the higher reflexes, e.g., turning over, compensatory and swimming. Small doses of the drug caused a depression of the reflexes and increasing doses brought about a tolerance.

INSTINCTS

Birds.—Watson (27), in the Carnegie Institute publications, has an historical and experimental study of homing. There is an excellent critical account of the various theories of homing, a brief summary of such instinctive activities of the noddy and sooty terns as have a bearing on the question, and a record of the experimental homing flights of these same birds in 1910 and 1913. Some of these flights covered as great a distance as 855 miles. In the same interesting field Cooke (5) has published, in a government bulletin, an account of migration with reference to the weather, the time of day, the distance covered, the routes, the rate of flying, etc. The maps are the most valuable part of this bulletin. They show both the general migration routes on the western continent and the special routes of different species.

Goodale (10) gave some young chicks to different capons who brooded them as hens would have done. There were slight differences in behavior but he says that, although the tests are not extensive, it would appear possible that the brooding instincts of the capon are not necessarily a female character.

Mammals.—The setting reactions of bird dogs to turtles is described by Bingham (2). Montané (18) tells of the instinctive reproductive behavior of an adult chimpanzee from Sierra Leone. The account is extended until after the birth of the young monkey. It is difficult to know whether articles on hibernation should be listed in this place or not. However, Rasmussen (22) has given a brief and valuable summary of the theories of this phenomenon and the paper includes a bibliography of 83 titles.

THE LEARNING PROCESS

Mammals.—Hamilton's laboratory in California probably offers the best facilities available for the study of monkeys in this country. In a Behavior Monograph, Yerkes (30) presents the results of his six months' work at this place. He used his multiple choice method, which has previously been described in this journal, with a *cynomolgos*, a *rhesus* and an *orang-utan*. It will be remembered that of nine entrance boxes, with from three to nine doors open in a prearranged order, the animals, in successive problems, were to choose the first door at the left, the second from the right, alternately the first door at the left and the second from the right, the middle door, etc.

The *cynomolgos* finished two problems, taking over 1000 trials for the second; the *rhesus* finished three and worked over a month on the fourth; and the *orang* finished the first but failed to solve the second in 1300 trials. Some supplementary tests were given and many interesting observations recorded. Professor Yerkes is disposed to insist, unduly it seems to the reviewer upon the basis of his experimental evidence, on ideational behavior—ideational control. He says: "Especially noteworthy, as evidences of ideation, in the results yielded by the multiple choice method are (1) the use by the *orang-utan* of several different methods in connection with each problem; (2) the suddenness of transition from method to method; (3) the final and perfect solution of problem 1 (by *orang-utan*) without diminution of

initial errors; (4) the dissociation of the act of turning in a circle from that of standing in front of a particular box."

A briefer description of this work is found in another article by the same author (31) and he gives a fuller account of the multiple choice method in the paper following (32). In *Science* (33) he presses a point which others have also advocated, that provision be made for a permanent field laboratory for the study of monkeys and apes.

Hamilton (11) this year continues his work on the perseverance (trial and error) reactions in primates and rodents. The apparatus had four doors of exit, only one of which in any trial permitted escape. This open door varied with every trial, but in a regular order. There could be no fixed reaction, no definite path to learn, in such a situation and Hamilton's interest lay in an attempt to analyze the varying responses. He found six general types of reactions which we have not space to enumerate, but he says that the different responses were less a species than an individual characteristic. The chief directive agencies are thought to be the spatial relations together with the pull which the recency and frequency of the activities in certain avenues exerted. In regard to recency and frequency the author maintains that, "These studies suggest a possibility which they by no means prove, that with descent of the phyletic scale the factor of recency increases in importance as a determinant of habit formation, whilst that of frequency relatively decreases."

The behavior of a group of monkeys involving the acquisition and control of some very awkward movements and unusual positions in getting food are described by Kempf (14). Another paper by the same author may be mentioned by title (15). And lastly among the many monkey studies appearing during the year is one by Furness (9) who reports upon his efforts to teach monkeys and apes to speak. Two other mammalian studies have been published: one by Meyers (17) on the importance of primacy in the learning of a pig, the other by Burtt (3) giving the results of his use of the multiple choice method with four rats.

Fish.—Maze problems have been used with fish before, but Churchill (4) contributes an account of his work with gold fish in a learning problem with a very simple maze.

QUESTIONS OF INHERITANCE

The behavior of stock and inbred rats was investigated by Mrs. Yerkes (29). She used the circular maze and the Yerkes discrimination box. On the whole the evidence seemed to show a greater facility in learning on the part of the stock (control) rats. The experimenter says: "The inbred rats showed an ability to form the same habits as the stock rats but they did it more slowly and with greater irregularities from day to day."

Another paper on inheritance is that of Bagg (1), called "Individual differences and family resemblances in animal behavior." He used 90 mice and the very simple maze of Cattell. Each individual was given 17 trials, but the first two trials are eliminated from the summaries because, the author says, they are so largely affected by chance. The method of experimentation was loose. The conclusions, which are based entirely on the mean variations in the time records, are, that the resemblances between individuals of the same litter are twice as great as the resemblances between the individuals of the entire group.

The behavior of chicks hatched from alcoholized eggs was the subject of research published by Fletcher, Cowan and Arlitt (8). By alcoholized eggs they mean eggs which had been treated with alcohol before incubating. Among the experiments were those concerned with light, pecking and drinking reactions, and maze learning. From the experiments, alcohol seems to have no specific effects. Such differences as were observed might easily have been due to malnutrition during hatching and could readily be produced by other agents.

GENERAL

Perhaps the most important paper that appeared during the year was Watson's (26) "Place of the conditioned reflex in psychology." The laboratory technique is carefully shown and then there follows a description of the general characteristics of the reflex with methods of dealing with them, ways of using the reflex to obtain differential reactions and finally the range and applicability of the method.

Peterson (21) contributed an additional explanation to the building up of a complex act or, perhaps one would better say, he elaborates a theory which has been implicit in other theories. Briefly, it is this: No partial response in a complex situation

can be viewed in isolation, as it grows out of what went before and looks forward in attitudinal impulses to what comes after it. Thus there are mutually reinforcing and inhibiting functions and overlapping of tendencies. And the adoption of the explanation of the complete response would help to explain the checked, impeded, inhibited behavior as well as that which shows reinforcement and also the elimination behavior incident to a successful reaction.

Behaviorism was the title of a paper contributed to the British association for Advancement of Science by Robinson (23). Swift (25) has an article entitled "Some developmental psychology in lower animals and man and its contribution to cer-, tain theories of adult mental tests." And Nesbit (20) has a valuable article, illustrated, describing the photographic outfit and technic for the fascinating undertaking of making wild animals take their own pictures.

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ON THE ABILITY OF ANIMALS TO KEEP TIME WITH AN EXTERNAL RHYTHM

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The habit of keeping time with an external rhythm, as in singing, dancing, and marching, is an interesting and important phase of human behavior. To what extent are similar habits found among the lower animals? A series of notes reporting observations that bear on this question have appeared in *Science*. But some of them have been uncritical, and the whole problem needs to be carefully analyzed.

To begin with, all non-rhythmic activities should be ruled out as having no bearing on the topic. Certain flocks of birds in flight turn this way and that with a speed and a simultaneity which are remarkable to witness. But their turnings do not recur in a regular rhythm; if they did so, they would constitute a very different and much more complex form of behavior.

As to rhythmic activities. All or nearly all animals keep time with slow rhythms, as the rhythm of day and night, and their ability to do so is an interesting topic in itself. But so far as behavior is concerned these slow rhythms belong in a different class from the quick rhythms here discussed, such as those of locomotion, of song, and of the flashing of fireflies. The slow rhythms often have nothing to do with the nervous system; in human consciousness they are not perceived as rhythms; and they may be left out of the present discussion.

As to the rhythms which are under discussion; there are some cases in which it is certain that animals do keep time with an external rhythm, but they are cases in which there is a direct mechanical connection between the moving parts of the animal and the external object with which it keeps time. A familiar example is the swinging of a canary on a swing perch. Some spiders (e.g., Argiope) swing on their webs in a way which seems to show that they time their movements with the rhythm of the web. Newman (8) and Wheeler (10) observed that certain Phalangidae gather in great clusters with their legs interlocked; when some individuals are disturbed they set up a swinging

movement which spreads to their neighbors, and gradually the members of the whole colony are brought into synchronous rhythmic movement. Peairs (9) reports that fall web-worm larvae engage in a rhythmic swaying movement which is synchronous in the whole colony; and he argues that it is probable that the rhythm is conveyed from larva to larva by slight movements of the web on which all rest. McDermott (5) mentions the same phenomenon in a web-worm (same species ?). In all these cases one can conceive how the synchronism is attained, without ascribing to the animals anything beyond their well-known powers; for the " imitated " rhythm is conveyed mechanically to the animal's body and to its muscles.

Without such a mechanical transfer, it is a question whether animals below man have ever been really observed to keep time with an external rhythm. A number of naturalists, as quoted below, claim to have observed such synchronous rhythms; but none of their reports are sufficiently detailed and exact to prove that their observations were free from illusion. There are three fertile sources of illusion in this matter, as follows: 1. The observer cannot give his attention equally to a number of objects at the same moment. It is impossible to watch even two moving objects and tell whether their movements are simultaneous, unless the objects are very conspicuous, or very close together, or both. This seems to account for the fact, e.g., that a man writes to me from California asserting that he has seen flocks of geese and of cranes in flight all moving their wings synchronously. Shull[1] makes a similar criticism of a supposed case of synchronism. 2. We all are prone to subjective accentuation, to a subjective rhythm, and to the illusion that this is an objective rhythm. 3. Many of these observers report a " high degree " of synchronism. Now, unless the synchronism is perfect, unless is includes *all* the animals under observation, the observer is liable to a statistical fallacy. For example, where a large number of fireflies are flashing at slightly different rates there must be a great amount of accidental synchronism; to determine whether there is a degree of synchronism not due to the laws of chance, one would need to make a statistical examination, unless the fireflies are all in perfect synchronism.

[1] Shull, A. F. The Stridulation of the Snowy Tree-cricket (*Oecanthus niveus*) *Canadian Entomologist*, 1907, **39**, 213-225.

Only one detailed and exact study of the problem is mentioned in any of these reports, or is known to the reviewer. It is Shull's[2] study of the chirping of crickets. Shull timed the chirping accurately in a large number of cases. He verified the law that the rate of chirping increases with the temperature, that at a given temperature nearly all the crickets chirp at almost exactly the same rate, so that there is necessarily a great deal of accidental synchronism. He singled out two individual crickets, to observe whether they really influenced each other and thus produced perfect synchronism, and he gives evidence indicating that this does occur, but the conclusion is stated with some reservation.

A number of naturalists write of fireflies flashing synchronously. But, of the contributors to the present discussion, none had observed this phenomenon more than once; Allard (1), Bumpus (quoted in 7 and in 3), and Morse (6) each had observed it once, and not under circumstances favoring critical observation. Blair (2) and McDermott (5) had never seen it themselves. Doctors S. O. Mast, W. M. Wheeler, and F. X. Williams tell me that they have never seen it. Laurent (4) says that many times in his own observations he has proved that what appeared to be synchronous flashing of fireflies was an illusion due to the twitching of his eyelids. And even in the reports that are given, the synchronism is ascribed to a large and indefinite number of fireflies, some reports even state definitely that the synchronism did not include all the individuals; hence none of the observations are known to have been free from the statistical fallacy mentioned above.

Wheeler (10) believes that a flock of pelicans in flight keep time with each other in their wing beats. In a letter which he kindly wrote to me in answer to inquiry, he says in part: "These birds fly in small flocks of four to eight individuals, if my memory serves me. These flocks are very compact, the birds flying in a single line coincident with the direction of flight, and not oblique as with geese. The beat of the wings was evidently set by the first bird, and sometimes there was an imperfect synchronism until the flock got under way. I am sure that the synchronism was not an illusion. I am also sure that it could not be ascribed to chance." Now, when geese fly in a

[2] *Op Cit.*

flock, each goose flaps its wings at its own rate, and thus is free to increase or decrease its speed; even so, the military precision with which geese form in line when moving at high speed through a fluid medium is a remarkable accomplishment. If pelicans can maintain a still closer line while at the same time each pelican beats its wings never faster and never slower than the leader, this is a most astonishing feat, more skillful, probably, than any synchronous rhythmic locomotor activity of human beings. If Wheeler is correct, his observations should certainly be verified and the phenomenon studied in detail by means of photographs and cinematograph films showing flocks of pelicans in flight.

Wheeler (10) suggests that animals exhibit " a kind of ' Einfühlung,' " but this term is surely inappropriate. He mentions also " a fine sense of rhythm." But it has not yet been proved that animals below man can clearly perceive a rhythm. An ex-cavalry officer writes to me that he regularly observed during parade that the moment the band began to play all the horses at once adjusted their step and forthwith kept perfect time with the music. If this observation were correct it would seem to show that each horse was clearly aware of the rhythm of his own step, of the rhythm of the music, and of the relation between the two. But probably the observation was not correct. On the other hand, if it can be proved that two animals come *gradually* into synchronous rhythmic activity and continue in perfect synchronism, as Shull[3] reports, with some reservation, for crickets, and Wheeler for pelicans, this does not prove that the animals perceive rhythm as such. The least assumption would seem to be that each cricket has two tendencies: each must have, *first*, a tendency to chirp in approximately a certain rhythm, the rate of which is not greatly different in different individuals; and this tendency of each animal to its own rhythm must be sufficiently plastic to yield to the *second*, which is an innate reflex tendency to chirp on receiving the auditory stimulus from the chirp of another cricket. But even this much has not yet been proved beyond question.[4]

[3] Op. cit.

[4] Since this review went to press the following additional note has appeared. Gates, F. C. Synchronism in the Flashing of Fireflies. Science, N. S., 1917, 46, 314. This writer arrives at the conclusion that "complete synchronism in the flashing of a group of fireflies is simply a very rare accident."

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SMITH'S "MIND IN ANIMALS" [1]

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The preface states that the book was written to present a brief account of the modes of procedure of animal psychology, its aims, trend and the general nature of the results obtained. Animal psychology concerns the systematic or experimental investigation of the brute mind.

The first chapter is entitled Protozoan Behavior. The variability or trial and error characteristic of primitive behavior is emphasized while the evidence in favor of retentiveness in these lower forms is not regarded as conclusive. Physiological or motor retentiveness evident in habit formation is discussed in the succeeding chapter. The author presents a good analysis and summary of the more important work on the maze or labyrinth problem.

The third chapter is entitled Associative Memory and Sensory Discrimination. Associative memory refers to the derivation by an object of a meaning or significance in virtue of its associative nexus with other activities. It is discussed as a criterion of mind, and its utility in studying discrimination and in testing the strength of a habit or instinct is noted. The larger part of the chapter is devoted to a review of the typical experiments on discrimination.

The following chapter on instinct discusses such topics as their initial imperfection, the generalized character of the stimulus, modifiability, periodicity, deferred instincts, etc. Instinct is identified more with the impulse than with the resultant acts. Instinct achieves certain results but the acts or means may vary. A unity of purpose runs throughout the series of acts. Instinct is thus not a mere chain of reflexes nor can it be explained except with difficulty in terms of reflexes and tropisms. The particular instinct of homing is the topic of Chapter V. Homing

[1] The Investigation of Mind in Animals. By E. M. SMITH. Cambridge, 1915, pp. lx+194.

is based upon an innate impulse to regain home, which must be supplemented by experience to achieve its end. The discussion is concerned primarily with the experimental factor and the factual material has been taken mainly from the work on ants, bees and wasps.

There is no general instinct for imitation, though some imitative acts may be termed instinctive. There is a good review of the literature on imitation in the higher animals. The author concludes: "That while under certain circumstances monkeys may, and do, imitate, their behavior as a whole can scarcely be characterized as imitative; nor does imitation appear to play any important part in their learning processes."

The final chapter is entitled The Evidence for Intelligence and for Ideas. It presents a critical analysis of the main experiments and arguments in favor of the existence of ideas and images in animals and the author concludes with the following statement: "Reviewing our evidence we may say that, it is by no means disproved that animals are intelligent and have 'ideas,' but, save possibly for the single exception of Hunter's method of 'delayed reactions,' no test as yet applied, completely excludes the possibility that animal learning is anything more than a process of association on the perceptuo-motor level."

The treatment does not pretend to be exhaustive. Technicalities and controversial questions have been omitted. The work is based almost wholly on experimental data; it reflects wide reading, clear analysis of the factual data and an orthodox judgment as to conclusions and interpretations. This book is well adapted to introduce and orient the general reader to the subject, and it may well serve as a text for the more elementary classes.

WOOD'S "THE FUNDUS OCULI OF BIRDS"[1]

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This handsome monograph is a useful addition to the literature of sense organs as well as to ornithology. It gives elaborate and extensively illustrated descriptions of the gross and microscopic structure of certain eye structures for a considerable number of birds. It is especially satisfactory to have such full accounts of the peculiar eye structures of birds, and a morphological basis is furnished for much needed experimental work on bird vision.

Besides the sections on methods, material, etc., there are the following chapters: 4. A Review of the Anatomy and Physiology of the Organs and Tissues seen in the Fundus Oculi of Birds; 6. Ophthalmoscopy of Birds; 7. Macroscopic Appearance of the Fundus Oculi of Birds in Prepared Specimens; 8. Photography of the Fundus in Prepared Eyeballs; 9. Effects of Domestication on the Fundus Oculi of Wild Species; 10. The Ophthalmoscopic and Macroscopic Appearance of the Fundus Oculi in Various Orders of Birds; 11. Classification of the Ocular Fundi of Birds; 12. The Ocular Fundus of Birds in its Relation to a Classification of Aves; 13. Relation of Reptilian to Avian Fundi.

The text figures are well executed and the numerous colored plates are beautifully done. The text print is good. Dr. Wood has been generous in financing the work himself. This interest of a clinician in the pure science bearings of his specialty deserves hearty commendation.

[1] The Fundus Oculi of Birds, Especially as Viewed by the Ophthalmoscope: A Study in Comparative Anatomy and Physiology. By Casey Albert Wood, M.D. Chicago, The Lakeside Press, 1917; 200 pp., 145 text figures and 60 colored plates.

HOLMES'S "ANIMAL BEHAVIOR"[1]

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The initial chapter contains an excellent account of the history of thought concerning animal intelligence from the time of Aristotle to the modern experimental movement. Then follows a sketch of the evolution of parental care. It develops from reproduction and the first stage involves the selection of a proper environment for the egg. An added step is found in the instinct to store food for the young. Active care for the egg is the next step and this interest in the egg is extended to the young. Parental care is a necessary condition for the development of the family, organized society, altruism, etc.

Three chapters are devoted to tropisms. Much illustrative material is given. The author accepts Loeb's reflex theory of orientation for the more primitive organisms, but trial and error is regarded as the predominant mode of adjustment. There is given an excellent sketch of the factors conditioning the reversals of tropisms and of the proposed theories of explanation.

Three chapters are devoted to intelligence and learning. Associative memory is the criterion of intelligence. Intelligence is derived from the instinctive activities and is not found among the Protozoa. Trial and error is the method of intelligent adaptation. The views of Spencer, Bain and Thorndike on the mechanism of selection are extensively criticised; the principle of congruity of responses is adopted. The primary acts mediate stimuli which excite secondary responses that in turn may either reinforce or interfere with the former. Selection and elimination are the resultants respectively of this reinforcement and interference. The author emphasizes the point that intelligent adaptiveness presupposes some degree of prior adaptiveness and this primary ingredient of purposive responsiveness is found in the congenital activities; in other words intelligence is necessarily a derivative of instinct.

[1] Studies in Animal Behavior. By S. J. Holmes, Badger, Boston, 1916, 266 pp.

Two chapters are devoted to the relation of form and behavior. Reviewing his own experiments in conjunction with those of Child, he concludes that the behavior of an organism plays but a subordinate though important rôle in the determination of its form. Under the title of Behavior of Cells the activity of many migratory and motile cells is cited. It is suggested that these activities are important in the development of form.

The chapter on Death Feigning describes the wide distribution of this instinct. There are two types,—the cataleptic and the paralytic. The former originated from the thigmotactic response, while the fear hypothesis can apply only to the latter.

The author discusses the sensory basis of sex recognition for various species. He emphasizes the factor of behavior in many forms. The sense used varies with the animal, while many senses may be employed in the higher forms. The fact of sex is important in the evolution of mind. Given asexual reproduction, mental evolution would have been different from what it was. For example, voice,—the instrument of language, functioned primarily as a sex call.

The final chapter describes some experiments on a monkey. The technique and the conclusions are similar to those of most studies on this animal.

In the preface we are told that the present volume is largely devoted to subjects with which the writer's own investigations in animal behavior have been more or less closely concerned. This fact explains the choice of topics and the organization of the book. It was probably intended more for supplementary reading than as a text. Naturally the biological aspects of behavior have been emphasized.

STORY OF GRANNY, THE MOUNTAIN SQUIRREL

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When collecting fossils around the west slope of the south ridge of Mount Wapta in 1911 rock squirrels began to come to the quarry we were opening. At lunch time we threw them bits of bread and crackers, and later carried up nuts to give them. They became very tame, and when we returned the following year (1912) one of them that we named Granny, because she apparently had two generations of young squirrels that came with her, would run up on our legs and shoulders, and if we did not promptly give her something to eat she would give a sharp chirp to call attention. One rainy day when crouched under a rubber blanket at lunch time, Granny came and seeing a cake of chocolate lying on my knee made a grab for it, running up my arm and over my shoulder so as to jump to the rocks behind. I made a grab for her, catching her by the end of the tail, which resulted in the snapping of her tail about midway. The following year (1913) she was about again as usual, being easily recognized by her stub tail.

We did not visit the quarry from 1913 until the latter part of July, 1917. Just after a blast had been fired, which was the signal to the squirrels that we were about to eat lunch, we saw two or three of them coming down from the cliffs above. When eating luncheon, Granny suddenly appeared at the edge of the quarry. I called her, "Granny," and whistled as we had in the years before. She immediately ran across the floor of the quarry, jumped up on my foot and ran up my leg, finally sitting up and begging for something to eat as she had done in 1913. There were three strange persons in the quarry, and she would not go near them for several days until she had had opportunity of getting acquainted. The striking feature of this incident is that this mountain squirrel should have remembered through a period of four years and at once ran and jumped up on me as she had been accustomed to doing previously.

Four other squirrels came, two of which were evidently full grown and a year or more old, and two young ones. As Granny disciplined them all when they became too familiar, we supposed that they were members of her immediate family.

After a week or more, Granny became very intimate with Mrs. Walcott and would jump into her lap and onto her shoulders, begging for food. She was entirely fearless, and would cling to a nut or a bit of chocolate and swing in the air until she secured the coveted bit.

When the squirrels first came, they were very thin and extremely active. After a month of feeding, Granny became so stout that she had great difficulty in jumping from rock to rock. Chocolate, nuts, bread and cookies seemed to agree with her, and the day we left the quarry a bountiful supply was placed under ledges of rock, so that they could all take it to their nests which were at the base of the cliffs, about 8,000 feet altitude.

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The Board of Editors has decided to discontinue publication of the Journal of Animal Behavior until the unfavorable conditions created by the war shall have ceased to exist.